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Germinative behaviour of *Acacia dealbata* Link, *Ailanthus altissima* (Mill.) Swingle and *Robinia pseudoacacia* L. in relation to fire and exploration of the regenerative niche of native species for the control of invaders

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ABSTRACT

Invasion of forest ecosystems by invader plants and forest fires are two of the most serious environmental problems in the world. Climate change is believed to strongly influence these processes, and the invasibility of invasive alien plants (IAPs) is likely to enhance landscape degradation. Therefore, it is urgent to study the germinative behaviour of invasive alien plants in relation to fire and detect possible barrier species of IAPs among native species. Tree species are usually the most damaging group of invasive alien plants. *Acacia dealbata* Link, *Ailanthus altissima* (Mill.) Swingle and *Robinia pseudoacacia* L. are 3 very damaging exotic invader trees in Europe and many other parts of the world. Therefore, the germination behaviour (germination percentage, viability pregermination, viability postgermination and germination rate) of these three species was experimentally studied against different products associated with fire (heat, smoke, ash and charcoal). The germination of *A. dealbata* and *R. pseudoacacia* was strongly stimulated by heat, while smoke, ash and charcoal barely changed the control values. None of these factors stimulated germination in *A. altissima*. Very high temperatures inhibited seed germination of the three species. The germination of *R. pseudoacacia* seeds was faster than that of *A. dealbata* and *A. altissima* seeds. Of the three species studied, *A. dealbata* and *R. pseudoacacia* have greater invasibility than *A. altissima*. A key role in invasive plant control research is to provide information to guide the decisions of forest managers involved in restoration. A possible solution is to use the biotic resistance of native vegetation to control biological invasions. For this purpose and based on extensive bibliographic revision, the regenerative niches of the three invasive species (germination, seedling growth and adult height) were compared with those of native European species to identify candidates for barrier species of IAPs between native species. Among the native species of Europe with characteristics in their regenerative niche suitable to successfully compete against these IAPs are tall shrub species such as *Adenocarpus lainzii* (Castrov.) Castrov., *Cytisus multiflorus* (L'Her.) or *Cytisus striatus* (Hill) Rothm. and tree species such as *Corylus colurna* L., *Pinus sylvestris* L. and *Quercus ilex* L. Therefore, the sowing of a good combination of shrub and tree species, selected according to their geographical distribution, could be an effective ecological

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measure to control the invasion of IAPs in burned areas. This information can be very valuable for implementing restoration measures in burned areas and should be verified with field experiments.

1. Introduction

Tree species are usually the most damaging group of invasive alien plants because they have the greatest ability to alter the composition of native species and ultimately alter the functioning of ecosystems (Wangen and Webster, 2006). In particular, soils colonised by IAPs often show increased proportions of organic carbon, total nitrogen, phosphorus and biomass through litterfall in comparison with those developed under the dominance of native species, making soils unsuitable for native vegetation (Vilà et al., 2011). *A. dealbata*, *A. altissima* and *R. pseudoacacia* are three of the most widely distributed invasive alien trees in the world. *A. dealbata* is native to southeast Australia and Tasmania and is an invader in southern Europe, the Americas and southern Africa (Rejmánek and Richardson, 2013). *A. altissima* is native to China and northern Vietnam and was introduced to France in the 18th century (Kowarik and Säumel, 2007). *R. pseudoacacia* is native to the central and eastern United States and was introduced to Europe in the 17th century (Kolbe et al., 2004). Today, all three species are present on all continents except Antarctica (Kowarik and Säumel, 2007; Lambdon et al., 2008; Weber and Gut, 2004).

A. dealbata, A. altissima and *R pseudoacacia* are among the 100 worst invasive species in Europe and "the top 100 worldwide woody plant invaders" threatening native vegetation (Cronk and Fuller, 1995; GEIB, 2006; Roy et al., 2009; Sanz Elorza et al., 2004). In several areas of Europe, the post-fire regeneration of *A. altissima* and *R. pseudoacacia* is so strong that few native species can compete with them (Maringer et al., 2012). *A. dealbata* causes threats to natural habitats in areas of Spain and Portugal, decreasing native biodiversity and homogenising communities (Aguiar et al., 2001; Lorenzo et al., 2011). The three species have allelopathic compounds in their tissues (Cierjacks et al., 2013; Kowarik and Säumel, 2007; Lorenzo et al., 2011) and have shown the ability to increase soil nitrate concentration and net nitrification rates in nutrient-poor soils, likely due to the high-quality leaf litter of *A. altissima* and the ability of *A. dealbata* and *R. pseudoacacia* to fix N_2 from the atmosphere (Gómez-Aparicio and Canham, 2008; Lorenzo et al., 2011; Rice et al., 2004; von Holle et al., 2013).

In many of the ecosystems invaded by these three species, fire is a recurring factor. Over time, fire has played an important modulating role in ecosystems due to its influence on the evolutionary processes of species (Trabaud, 1992), and it is present in many ecosystems on Earth (Pausas and Keeley, 2009). For example, southern Europe is one of the regions of the planet most susceptible to forest fires (Fernández-García et al., 2020). Around the world and especially in these areas, climate change will favour more severe and recurring forest fires due to the reduction in rainfall and the increase in global temperature (Flannigan et al., 2005). Climate change could benefit exotic species over native species (Grigulis et al., 2005; Myers et al., 2004; Riveiro et al., 2019) directly by creating disturbed areas susceptible to being colonised earlier by invasive alien plants than by native species. Indirectly, this favours increasingly severe and recurring forest fires (Reyes et al., 2018). Changes in fire regimes together with the gradual loss of native species create opportunities for new species, including IAPs, to colonise and dominate in a new area, producing positive feedback between IAPs and the cycle of fire (Brooks et al., 2004; D'Antonio, 2000).

To reduce the invasibility of IAPs, it is necessary to know how they work in environments where they are most likely to be successful: fire-prone environments. Plants use various strategies, both in adulthood and in the form of a propagule, to increase survival (Craine, 2009). As a propagule, a widely used strategy is seed dormancy for long periods of time, probably to escape unfavourable conditions for seedling development, and dormancy breakdown through different stimuli when conditions are more conducive to plant survival. Forest fires leave environments free of competition and with a large amount of resources for plant growth (Reyes et al., 2018). High temperatures from fires break seed dormancy by breaking down the hard, waterproof covering of many seeds (Cruz et al., 2017; Rivas et al., 2006; Riveiro et al., 2020). The germination and establishment of species, whether native or invasive, sometimes depend on specific stimuli (Goets et al., 2017). The three species studied are fast-growing and early-maturing trees, and they produce numerous seeds with hard cover (Feret, 1973; Gilbert, 1959; Masaka and Yamada, 2009; Takahashi et al., 2008). These seeds can persist stored in the soil for long periods (Luken and Goessling, 1995; Praciak et al., 2013) and show physical dormancy due to their hard and waterproof cover (Geldenhuys, 1994; Milton and Hall, 1981). After breaking the seed coat, the seeds can be imbibed if there is some water on the ground and they come out of dormancy (Aveyard and Mitchell, 1968; Baskin and Baskin, 2014; Clemens et al., 1977; Graves, 1990).

IAPs with large persistent seed banks complicate the management of areas that these species invade due to prolonged seed viability (D'Antonio and Meyerson, 2002; Suding et al., 2004). Since the processes of initial colonisation are decisive in the paths of success or failure followed by the populations of the competing species (Hunt et al., 1999), it is necessary to study seed germination after forest fire to highlight the key aspects of the regenerative niche of invasive alien plants compared to native species in the early stages of succession in burned areas.

There are studies on other species and fire but few on these three species in invaded areas (Burrows et al., 2018; Pedrol et al., 2018; Rebbeck et al., 2019). Most works only analyse the effect of temperature thresholds. However, there are other fire factors that also modify the germination patterns of many species, for example, smoke in many species in Australia (Arán et al., 2013; Auld and O'Connell, 1991; Brown et al., 1994; Cruz et al., 2017; Morris, 2000) and in some of the Mediterranean basins (Baeza and Vallejo, 2006; Çatav et al., 2014; Crosti et al., 2006; Reyes and Trabaud, 2009). Ash and charcoal are other fire factors that increase or decrease the germination of some species (González-Rabanal et al., 1994; González-Rabanal and Casal, 1995). Additionally, most germination studies are focused only on germination percentage and do not centre on key characteristics such as seed viability and germination

rate. The seed viability before and after germination and the germination speed of IAPs in relation to fire factors may provide important ecological insight into the invasiveness of the species. This information is very valuable in helping to provide knowledge about the germinative behaviour of species and facilitate the design of management measures appropriate to the productive or conservation purposes being considered.

To provide useful information for forest managers involved in the restoration of burned areas, it is necessary to investigate the characteristics of both the regenerative niche of invasive species and that of native vegetation that may offer biotic resistance to invasion. The regeneration niche is the minimum requirement necessary for a mature individual to be successfully replaced by another mature individual of the next generation (Grubb, 1977). Germination rates, seedling growth and adult height are key characteristics of the regenerative niche that will condition the survival and abundance of populations of species after fire, both for IAPs and native species (Donohue et al., 2010; Lloret and Zedler, 2009; Marañón et al., 2004). Biotic resistance via competition with native species is an ecologically very interesting but still little explored control measure (Brose, 2010; Conedera et al., 2010; Maringer et al., 2012). Germination behaviour in relation to fires (percentage, time and trigger factors), seedling height in early years of life and maximum height of adult plants are key characteristics of that species capable of eliminating or reducing the emergence of IAP seedlings in postfire scenarios. Early germination allows seedlings to develop quickly and compete for resources (light, water, and nutrients). Abundant germination, whether mediated or not by a fire stimulus, would achieve rapid covering of the soil and the accumulation of resources, especially light above the ground and water below it. The rapid growth in height would allow the development of canopies in layers higher than those of the IAPs, greatly reducing the amount of light available to them. The native species that present these traits can be called barrier species (BSs) of IAPs. Therefore, it is urgent to review the knowledge that exists on the regenerative niche of native species and compare them with the regenerative niches of *A. dealbata*, *A. altissima* and *R. pseudoacacia* to provide ecological solutions that are effective, cost-effective and sustainable over time. To shed light on these issues, we propose the following aims:

i) Evaluate the role of fire, through its main characteristics (heat, smoke, ash and charcoal), on the viability of seeds, percentage and rate of germination of *A. dealbata*, *A. altissima* and *R. pseudoacacia* and identify which treatments help reduce its invasive power.
ii) Compare the germinative responses of these three species to fire with those of other species native to Europe (through a bibliographic review) to identify possible native candidate species to act as BSs of IAPs.

2. Materials and methods

2.1. Biological material

The fruits (pods and samaras) of *A. dealbata*, *A. altissima* and *R. pseudoacacia* used in this work were picked in naturalised populations in SW Europe during their dispersal season. In the laboratory, the seeds were extracted and cleaned manually, and seeds with a healthy appearance were selected and placed in paper bags. The seeds of *A. dealbata* and *A. altissima* were collected by the authors in forest areas invaded by these species around the city of Ourense (Spain). The seeds of *R. pseudoacacia* were collected by a company specialised in seed harvest and conservation in the Ebro Valley (Spain). The seeds of *A. altissima* were kept cold (4 °C) for more than one year. The seeds of *A. dealbata* and *R. pseudoacacia* were stored under laboratory conditions at approximately 25 °C for at least one year until the start of the experiments.

2.2. Germination and viability

Objective one was to test fire-related factors through heat, smoke, ash and charcoal. We selected *Ulex europaeus* L. as the material to burn and generate smoke, ash and charcoal, as it is one of the most abundant species in shrublands and understories of woodlands of SW Europe (Puentes et al., 2016; Reyes et al., 2000).

A forced air oven (IDL-FI-120) was used to apply thermal shocks to the seeds in dry conditions. The temperatures tested were 80 °C, 110 °C, 150 °C and 200 °C, and the exposure times were 5 and 10 min. Temperatures and exposure times correspond to those registered at different soil depths during forest fires and experimental burns by Dunn and DeBano (1977) in chaparrals of California, by Trabaud (1979) in French garrigues, by Díaz-Fierros et al. (1990) in shrublands of northwestern Spain, and by Auld and O'Connell (1991) and Bradstock and Auld (1995) in Mediterranean ecosystems of southeastern Australia.

Smoke treatment was carried out with the Smoke 2000 applicator (Casal et al., 2001) based on the methodology proposed by de Lange and Boucher (1990). The device consists of a smoke generator, a cooling tube and a 2.5 m^3 chamber acting as a smoke receiver. This system was used so that the smoke entered the seeds at room temperature, allowing us to perfectly isolate the effect of the smoke (Reyes and Trabaud, 2009). At the moment in which smoke saturation conditions were reached, the seeds were placed in the chamber for 5, 10 and 15 min (Rivas et al., 2006). Each smoke and thermal shock replica was independently introduced into the stove or smoke chamber.

The applied ash treatments followed the criteria of Soto et al. (1997). These quantities correspond to multiples of the quantities collected from controlled burning conducted in an Atlantic shrubland of southwestern Europe. These quantities were Ash1 (0.027 g/Petri dish, 43.5 kg ha^{-1}), Ash2 (0.055 g/Petri dish, 87 kg ha^{-1}) and Ash3 (0.11 g/Petri dish, 174 kg ha^{-1}). Ash was obtained from the total combustion and charcoal from the partial combustion (~20 min) of dried material (principally branches and leaves) of *U. europaeus*. Ash was separated from charcoal and other fractions with a sized 0.4 mm mesh sieve, and charcoal was separated from the rest of the charred material with a sized 2.1 mm mesh sieve. Ash and charcoal were then placed on respective dishes, and the seeds were sown on top. The seeds were incubated in Petri dishes in 0.26 g (411 kg ha^{-1}) of charcoal. This is the equivalent amount of

charcoal measured by Ohlson and Tryterud (2000) after experimental fires in the boreal forests of Scandinavia and is the dose used in previous work.

After applying the treatments, the treated and control seeds were kept in an incubation chamber (Climas AGP890). For each species, 5 replicates of 25 seeds per Petri dish were prepared following ISTA standards (ISTA, 2005). Every Petri dish was watered with

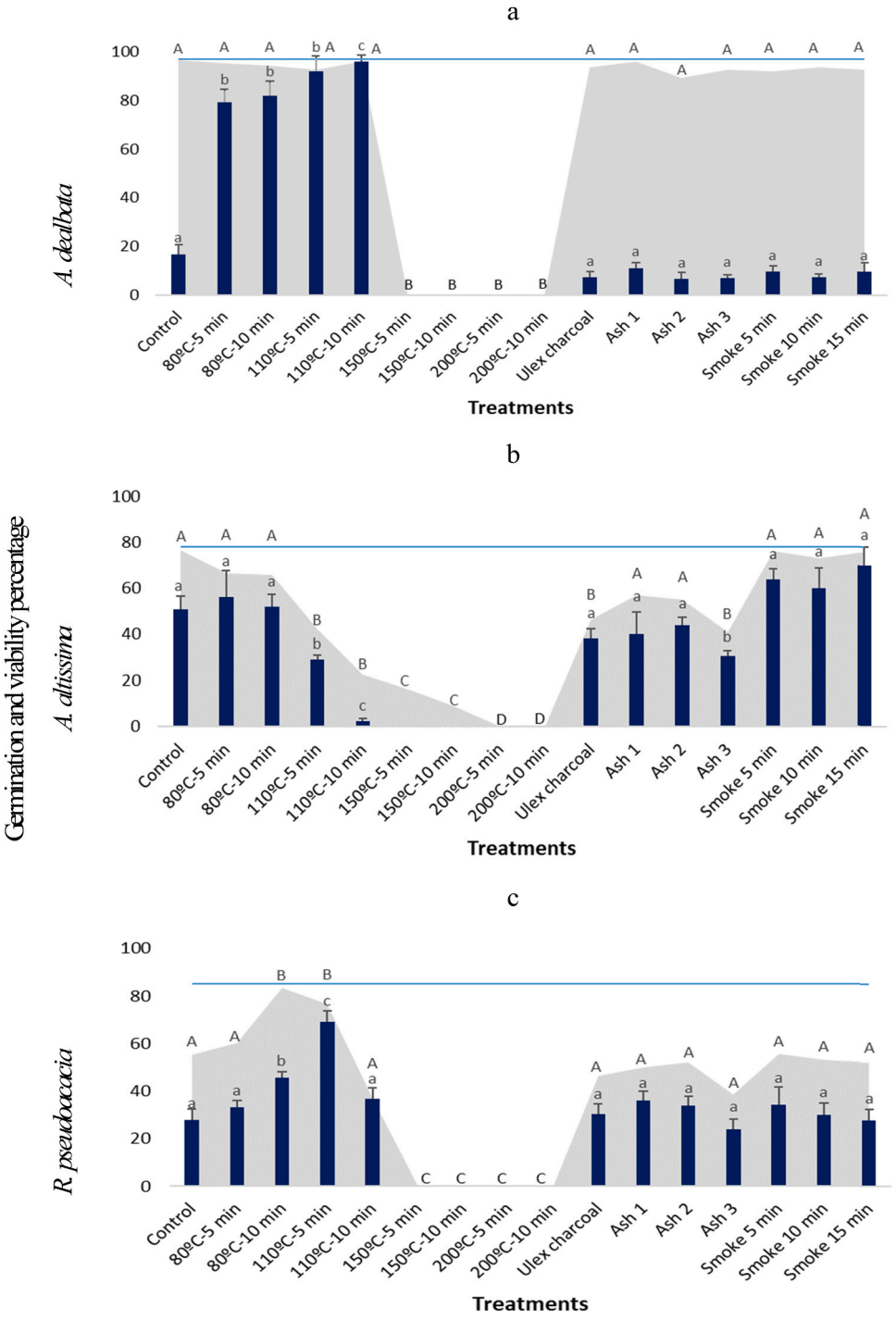

Fig. 1. Pregermination viability (blue line), postgermination viability (grey area) and germination percentages (blue bars; mean ± SE) reached by *A. dealbata* (a), *A. altissima* (b) and *R. pseudoacacia* (c) seeds. Lowercase letters on the bars indicate significant differences between the treatments and the control treatment. Capital letters in an area indicate significant differences between the treatments and control treatment. wd: without data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5 ml of distilled water and thereafter with a suitable amount of water needed to allow germination of the seeds. The incubation photoperiod was 16 h of light at 24 °C and 8 h of darkness at 16 °C to simulate the thermophotoperiod that coincides with that registered in the northwest of the Iberian Peninsula during summer. Germination was monitored three times every week for 30 days.

The viability after showing (pregermination viability) and the viability of ungerminated seeds after germination tests (post-germination viability) were checked with a tetrazolium test. For this test, a solution of 2,3,5-triphenyl-tetrazolium chloride (colourless) was used as an indicator of the reduction processes that occur in living cells (Salazar Mercado and Gélvez Manrique, 2015). The seeds were embedded in this solution at a 1% concentration. Through oxidation-reduction processes, living tissues convert this salt into a compound called formazan (reddish), which allows us to visually distinguish living from dead parts of seeds. The seeds of the three species were scarified due to their hard cover and thus facilitated the entry of the solution to the interior of the seeds. Five replicates were carried out, as in the germination test, with the ungerminated seeds after 30 days of the germination test. The seeds with the tetrazolium solution were kept for 48 h in the dark, and subsequently, the remaining viable seeds of each treatment applied to the 3 species were counted.

The pregermination viability, the postgermination viability, the percentage of germination, and the germination rate through T_{50} (average time it takes to produce 50% of the total germination) were calculated. The T_{50} value could not be calculated in those treatments with a germination percentage of 0.

2.3. Statistical procedures

The responses to fire of *A. dealbata*, *A. altissima* and *R. pseudoacacia* were statistically analysed. Viability after germination, percentage of germination and T_{50} were analysed to check if they fulfilled a normal distribution of the data. We performed multivariate general linear models (GLMs) on the dependent variables of viability, percentage of germination and T_{50} and the fixed factor species and treatments to identify significant differences and/or significant interactions between factors. These analyses detected significant interactions between the factors when the dependent variables, viability and germination percentage, were analysed but were not detected with the T_{50} variable. Then, univariate GLMs were carried out with a 0.05 level of significance to test the effects of fire treatments in each species. Treatments with less than three replicates over 0% germination were removed from the T50 analysis. Tukey tests were used for a posteriori comparison. To perform these statistics, IBM SPSS Statistics 24 was used.

2.4. Bibliographic review of possible native barrier species

Objective two was to complete an extensive bibliographic review of published works on the regenerative niche of 47 representative tall shrub and tree species native to Europe living in fire-prone environments. To achieve this, germination percentage, T_{50} and temporal patron data (total days seeds took to germinate) were analysed. Together with the aforementioned data, fire factors that could stimulate germination of these species with respect to the control were also collected, and their values were recorded. These data were tabulated and compared with the data from this work.

In addition, information was sought for these species regarding their average height in adulthood and the average height of the seedlings or basal sprouts after a disturbance (fire or cut). Both heights of the adult and young individuals were compared with the adult and young heights of the IAPs studied to determine which native species could be eliminated by competitive exclusion of the invaders. These native species would compete effectively for resources, especially for light.

3. Results

3.1. Reproductive behaviour of invasive species

The viability of seeds before starting the germination test was very high in all three species, 97% in *A. dealbata,* 78% in *A. altissima* and 85% in *R. pseudoacacia* (Fig. 1). The viability of the seeds that did not germinate after 30 days of incubation (postgermination viability) differed greatly depending on the species and the treatments received ($p < 0.001$). Multivariate GLM detected significant differences between *A. dealbata* and the other two species ($p < 0.001$). The viability of the *A. dealbata* seeds remained very high, close to the pre-germination viability, even in the seeds subjected to thermal shocks of 110 °C, and only thermal shocks of 150 °C and higher significantly reduced the viability of seeds. The control seeds and those subjected to carbon, ash and smoke treatments also maintained their high viability and did not show significant differences with the viability of the control seeds. Although *A. dealbata* seeds had high viability, their germination percentage was notably lower than the viability percentage.

The postgermination viability of the *A. altissima* seeds gradually and significantly declined as the thermal shocks were more severe and the ash concentration was higher ($p < 0.001$). The 110 °C-5 min and 110 °C-10 min treatments reduced viability to half the viability of the control seeds. Treatments at 150 °C for 5 min and 150 °C for 10 min reduced the viability to a quarter and a fifth, respectively, and the viability of the seeds subjected to 200 °C for 5 min and 200 °C for 10 min became zero. Increasing concentrations of ash significantly decreased the viability of *A. altissima* seeds ($p < 0.001$) from approximately 56% with Ash1 and Ash2 to 41% with Ash3. Post-germination viability of *R. pseudoacacia* seeds decreased with respect to pre-germination viability with all treatments except those that produced germination stimulation, that is, 80 °C-10 min and 110 °C-5 min. This reduction in viability percentage occurred after 30 days of incubation of the seeds in an environment with sufficient humidity to allow germination. On the other hand, the viability of the seeds subjected to thermal shocks between 150 °C and 5 min and 200 °C-10 min was completely annulled.

Germination percentages varied depending on species and treatment (Fig. 1). On the one hand, multivariate GLM detected significant differences between *A. altissima* and the other two species ($p < 0.001$). On the other hand, statistical analyses also detected significant

differences between the control treatment and some fire factors in the three species studied ($p < 0.001$). *A. dealbata* reached 16.8% germination in the control treatment (Fig. 1a), *A. altissima* reached 50.8% (Fig. 1b), and the value of *R. pseudoacacia* was 27.9% (Fig. 1c).

Heat treatments from 80 °C-5 min to 110 °C-10 min significantly increased germination percentages ($p < 0.001$) in *A. dealbata,* reaching values of approximately 80%, and the percentage of germinated seeds was very close to the percentage of viable seeds. The germination of *A. altissima* was not stimulated by thermal shocks. Severe heat treatments, from 150 °C-5 min to 200 °C-10 min, significantly inhibited the germination of the three studied species ($p < 0.001$), and viability was zero or close to zero. In addition, the 110 °C-5 min and 110 °C-10 min treatments greatly decreased *A. altissima* germination ($p < 0.001$) and seed viability.

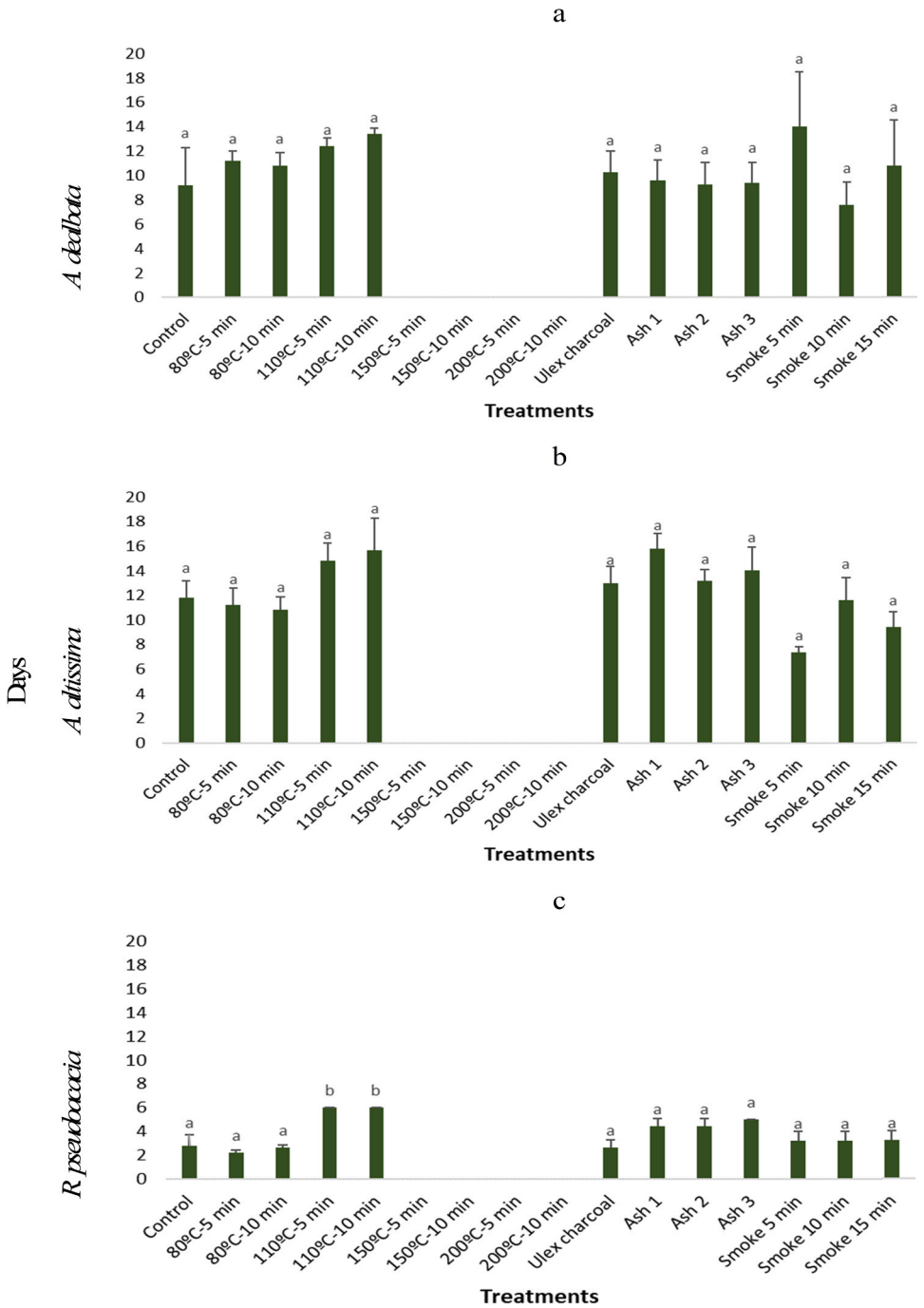

Fig. 2. T_{50} (mean ± SE) reached by *A. dealbata* (a), *A. altissima* (b) and *R. pseudoacacia* (c) seeds. Treatments without germination have no T_{50} value. Different letters on the bars indicate significant differences between the fire treatments and the control treatment. wd: without data.

Table 1
Germination percentages, T_{50} values and total days it takes to germinate (temporal patron) tall shrub species and tree species native to Europe. The control values and values achieved with the most stimulating treatment of each species are indicated, alongside the family, country of seed collection and bibliographic reference.

Species	Family	% Control	T_{50} Control	Temporal patron (days)	Stimulating treatment	% Treatment	T_{50}	Time (days)	Country	Reference
A. lainzii	Fabaceae	5.3	30	150	100º-7.5 min	99.3	14	150	Spain	(Boedo, 2002)
A. glutinosa[a]	Betulaceae	10 ± 1	–	84	–	–	–	–	Australia	(Crosti et al., 2006)
A. unedo	Ericaceae	90	18	52	–	–	–	–	Greece	(Bertsouklis and Papafotiou, 2013)
B. pendula[a]	Betulaceae	33.5	15	40	–	–	–	–	Spain	(Reyes et al., 1997)
C. sativa	Fagaceae	58	53	130	–	–	–	–	France	(Bacilieri et al., 1993)
C. intermedia[a]	Fabaceae	21	–	90	80º-5 min	88	–	–	Spain	(Buhk and Hensen, 2006)
C. silique	Fabaceae	78.5	10	60	100º-5 min	98.9	–	60	Spain	(Ortiz et al., 1995)
C. laurifolius	Cistaceae	68	–	42	–	–	–	42	Spain	(Rosario Nuñez et al., 2003)
C. colurna	Betulaceae	36.3	–	30	Pretreatment	91.3	–	30	Turkey	(Arslan, 2020)
C. multiflorus[a]	Fabaceae	15 ± 3.8	16	72[b]	100º-7.5 min	67.3 ± 9.8	30[b]	122[b]	Spain	(Reyes and Boedo, 2001)
C. reverchonii[a]	Fabaceae	4.6	24	60	90º-10 min	80.3	37.5	60	Spain	(Herranz et al., 1998)
C. scoparius	Fabaceae	3.2 ± 3.4	28.3	99[b]	80º-10 min	27.2 ± 12.8	62.6	152[b]	Spain	(Cruz et al., 2020)
		5 ± 1.6	-	100	110º-5 min	25 ± 3.9	-	100	England	(Hanley, 2009)
C. striatus	Fabaceae	11.2 ± 7.2	13.4	70[b]	110º-10 min	57.6 ± 9.2	40.6[b]	92[b]	Spain	(Rivas et al., 2006)
		12	22	60	120º-10 min	76	36.5	60	Spain	(Herranz et al., 1998)
E. australis	Ericaceae	26 ± 3.4	–	76	70º-1 h	59.8 ± 4.3	–	76	Spain	(Cruz et al., 2003)
F. excelsior	Oleaceae	24.5	–	98	–	–	–	–	Sweden	(Tapper, 1992)
F. ornus	Oleaceae	20 ± 4.7	–	84	–	–	–	–	Australia	(Crosti et al., 2006)
G. florida[a]	Fabaceae	23	–	42	100 ºC-5 min	46	–	42	Spain	(Núñez-Regueira et al., 2003)
G. scorpius[a]	Fabaceae	28 ± 8.7	22	–	–	–	–	–	Spain	(Reyes and Trabaud, 2009)
H. atriplicifolium	Cistaceae	9	–	90	100º-30 min	65	–	–	Spain	(Buhk and Hensen, 2006)
H. lasianthum[a]	Cistaceae	6.2 ± 1.7	7	–	120º-5 min	26 ± 10.5	28	–	Spain	(Valbuena et al., 2019)
J. oxycedrus	Cupressaceae	14.6 ± 3.8	–	84	–	–	–	–	Australia	(Crosti et al., 2006)
O. europaea	Oleaceae	15.8	–	82.6	Scarification	85.8	–	35	Ethiopia	(Bezu Bedada et al., 2018)
P. latifolia	Oleaceae	91	35	–	–	–	–	–	Spain	(Herranz et al., 2006)
P. brutia[a]	Pinaceae	92.5	15.7	85	–	–	–	–	Greece	(Skordilis and Thanos, 1995)
P. halepensis[a]	Pinaceae	91.4	17	42	–	–	–	–	Spain	(Núñez and Calvo, 2000)
P. nigra[a]	Pinaceae	91 ± 2.6	4	14	–	–	–	–	Spain	(Alvarez et al., 2007)
P. pinaster[a]	Pinaceae	97 ± 1.5	14.4	41	–	–	–	–	Spain	(Alvarez et al., 2007)
		67 ± 15	13	-					Spain	(Valbuena et al., 2019)
P. pinea	Pinaceae	25.6 ± 12.8	16.8	–	Humus exudate	49.5 ± 20.2	16.1	–	Spain	(Calvo et al., 2013a)
P. radiata[a]	Pinaceae	65	17	31	–	–	–	–	Spain	(Reyes and Casal, 2001)
P. sylvestris	Pinaceae	92.5	13	42	–	–	–	–	Spain	(Núñez and Calvo, 2000)
P. alba[a]	Salicaceae	88	14	–	–	–	–	–	Spain	(González et al., 2010)
P. tremula	Salicaceae	98	44	63	–	–	–	–	Finland	(Latva-Karjanmaa et al., 2003)
P. tridentatum[a]	Fabaceae	15 ± 6.1	28.2	66[b]	110º-5 min	64.8 ± 12.5	40.6[b]	82[b]	Spain	(Rivas et al., 2006)
		11 ± 5.2	22	-	120º-5 min	79 ± 16.8	44	-	Spain	(Valbuena et al., 2019)
Q. ilex	Fagaceae	97.3	68	154	–	–	–	–	Spain	(Reyes and Casal, 2006)
Q. pubescens	Fagaceae	92	24	130	–	–	–	–	France	(Bacilieri et al., 1993)
Q. pyrenaica	Fagaceae	65.6	55	343	Ash	80.2 ± 4.6	44	196	Spain	(Reyes and Casal, 2006)
Q. robur	Fagaceae	59.2	77	287	Smoke 10 min	77.2 ± 5.9	86	231	Spain	(Reyes and Casal, 2006)
S. atrocinerea	Salicaceae	86.4 ± 3.3	4	8[b]	–	–	–	–	Spain	(Cruz et al., 2020)
S. junceum[a]	Fabaceae	49 ± 9.1	32	-	110º-5 min	80 ± 6.7	24	-	Spain	(Reyes and Trabaud, 2009)
		40 ± 2.7	-	100	95º-5 min	69 ± 6.2	-	100	England	(Hanley, 2009)
S. aria	Rosaceae	38.5	–	170	–	–	–	–	France	(Devillez et al., 1980)
S. aucuparia	Rosaceae	89.5	–	150	–	–	–	–	England	(Raspé et al., 2000)
S. domestica	Rosaceae	76	–	160	–	–	–	–	Czech Republic	(Prknová, 2015)
S. torminalis	Rosaceae	42	–	150	–	–	–	–	Iran	(Espahbodi et al., 2007)

(*continued on next page*)

Table 1 (*continued*)

Species	Family	% Control	T_{50} Control	Temporal patron (days)	Stimulating treatment	% Treatment	T_{50}	Time (days)	Country	Reference
U. glabra	Ulmaceae	91.5	7	14	–	–	–	–	Turkey	(Çiçek and Tilki, 2006)
U. europaeus[a]	Fabaceae	52 ± 10.2	17.8	82	80º-10 min	96.8 ± 3.3	16.8	61	Spain	(Rivas, 2015)
		50 ± 1.6	-	100	110º-5 min	97 ± 2	-	100	France	(Hanley, 2009)
		64 ± 4.8	-	100	80º/95º-5 min	90 ± 3.1	-	100	England	
U. minor[a]	Fabaceae	2.7 ± 1.6	–	100	110º-5 min	73.3 ± 2.1	–	100	England	(Hanley, 2009)
U. parviflorus[a]	Fabaceae	11	43	100	80º-10 min	79.1	31	100	Spain	(Baeza and Roy, 2008)

[a] Species not included in the text with the full scientific name: *Alnus glutinosa* (L.) Gaertn., *Betula pendula* ROTH, *Calicotome intermedia* C.Presl, *Cytisus multiflorus* (LHér.) Sweet, *Cytisus reverchonii* (Degen & Hervier), *Genista florida* L., *Genista scorpius* (L.) DC., *Halimium lasianthum* (Lam.) Spach, *Pinus brutia* Ten., *Pinus halepensis* Mill., *Pinus nigra* J.F.Arnold, *Pinus pinaster* Aiton, *Pinus radiata* D.Don, *Populus alba* L., *Pterospartum tridentatum* (L.) Willk., *Spartium junceum* L., *Ulex europaeus* L., *Ulex minor* Roth, *Ulex parviflorus* Pourr.

[b] Data not previously published.

Instead, *R. pseudoacacia* germination was stimulated by temperatures between 80 °C-10 min and 110 °C-5 min ($p < 0{,}001$), and 69% of the maximum reached germination as did approximately 30% of viable seeds that did not germinate with the control under the 80 °C-5 min and 80 °C-10 min treatments.

Smoke treatments and *Ulex* charcoal treatment had the same effect on different species: no modification of the control germination. The ash treatments also did not modify the control germination of the three species with the sole exception of the Ash3 treatment in *A. altissima*, which significantly reduced germination to 29.6% ($p < 0.002$).

In the three studied species, the time required for germination reached 50% of its final value, following similar patterns with different average values. The germination time of the control treatment in *A. dealbata* was 9 days, 12 days in *A. altissima* and 3 days in *R. pseudoacacia* (Fig. 2).

The T_{50} of all treatments performed on *A. dealbata, A. altissima* and *R. pseudoacacia* seeds showed no significant differences from the control treatment (Fig. 2), and their average T_{50} values were 11 days in *A. dealbata*, 12 days in *A. altissima* and 4 days in *R. pseudoacacia* ($p = 0.135$).

3.2. Regenerative niche of possible barrier species of IAP

3.2.1. Native species candidates for IAP barrier species

To identify potential barrier species of the 3 IAPs studied, we carried out a literature review, focusing on 47 species from 11 families (Table 1). All of them are native and abundant species in different regions of Europe, living in areas prone to forest fires. As a first selection feature, we looked at shrubs of high bearing and trees. Second, we analysed their germination behaviour in relation to fire and the height of their seedlings in the first years of life as well as the height reached by adult individuals.

Of the 47 species selected, 14 species belonged to the Fabaceae family, 7 species to Pinaceae, 5 to Fagaceae, 4 to Oleaceae and Rosaceae, 3 species to Betulaceae, Cistaceae and Salicaceae, 2 to Ericaceae and 1 species to both Cupresaceae and Ulmaceae.

These species often exhibit different fire behaviours depending on the family to which they belong. The Fabaceae family has controlled germination between 5% and 64%, and heat treatments can reach values close to 98% in many of the shrub species studied. The only revised tree species in the Fabaceae family is *Ceratonia siliqua* L., with high control germination (78.5%) and close to 100% with high temperatures. In general, the Pinaceae family has control germination percentages greater than 90% and low values of mean germination time (15 days). Among the Fagaceae family, *Quercus ilex* L. and *Quercus pubescens* Willd. have control germination greater than 90%, and *Quercus pyrenaica* Willd., *Quercus robur* L. and *Castanea sativa* Mill. have control germination greater than 60%. The Oleaceae family, *Fraxinus excelsior* L., *Fraxinus ornus* L. and *Olea europaea* L. have low control germination (16–25%), but the germination of *O. europaea* increases to approximately 90% with the scarification of its seeds. *Phillyrea latifolia* L. stands out in this family for having germination control greater than 90%. In the Rosaceae family, *Sorbus aria* (L.) Crantz and *Sorbus torminalis* (L.) Crantz have controlled germination of approximately 40%, *Sorbus domestica* L. 76% and *Sorbus aucuparia* L. 90%. The Salicaceae family, with two species of the genus Populus and one of Salix, has very high control germination, between 86% and 98%. In the Cistaceae family, the two species of the genus Halimium have very low germination and increase with thermal shocks, so *Halimium atriplicifolium* (Lam.) Spach reached 65% germination at 100 °C for 30 min. On the other hand, *Cistus laurifolius* L. presented 68% control germination and was not modified with heat. The Betulaceae family has low control germination, less than 36%, producing great stimulation with hormone pretreatment and heat in *Corylus colurna* L. (91%). In the Ericaceae family, there are two different behaviours. While *Arbutus unedo* L. has a high control germination (90%), *Erica australis* L. has a low control germination (26%) but is stimulated by heat reaching 60% with 70 °C-60 min. Finally, *Juniperus oxycedrus* L. has low control germination (15%), and *Ulmus glabra* Huds. has a high germination rate (91%) and a short time (14 days).

Once the germination of these species in relation to fire was analysed, we sought information on the height of seedlings at 1 or 2 years of life and the height of adult individuals (Table 2). In the 36 species for which information was found, the abundance of species of the Fabaceae family stands out. The seedlings of *Adenocarpus lainzii* (Castrov.) Castrov., *Cytisus scoparius* (L.) Link and *Cytisus striatus* (Hill) Rothm. grow rapidly and achieve a remarkable height in their first year, reaching 1 m, and their height in adulthood reaches 2–3 m. The other species in this family have an average height of 60 cm in one-year-old seedlings, and in adulthood, only *C. silicua* reaches 10 m in height. In general, the selected Pinaceae family has slower growth, and the height of the one-year-old seedlings is low (less than 40 cm). However, *Pinus sylvestris* L. and *Pinus pinea* L. seedlings reach taller heights (153 and 200 cm at two years, respectively). As adults, the individuals of *P. sylvestris* and *P. pinea* also reach considerable heights (30 and 40 m, respectively). Fagaceae family members have low seedling heights, except *Q. ilex*, which stands out with a height of almost 92 cm in its first year of growth. As adults, *Q. ilex*, *Q. robur* and *C. sativa* are the highest species in this group with sizes between 25 and 30 m. The one-year-old seedlings of the Oleaceae family have heights close to 1 m, and the seedlings of *F. ornus* reach 94 cm, those of *P. latifolia* reach 98 cm and the 4-year seedlings of *O. europaea* reach 230 cm. In the adult stage, these three species only reach between 8 and 10 m, but *F. excelsior*, with lower seedlings, can measure 40 m in height. The Rosaceae family has a height in its first year of between 40 and 59 cm and between 15 and 25 m when they are adults. The represented species of the Betulaceae family have heights between 75 and 108 cm in their first year, and *C. colurna* at 6 years can reach 430 cm. The height of adult individuals is between 25 and 30 m. The Cistaceae family has a very low height in the first year, reaching only 15 cm, and when these species are adults, they do not usually exceed 2 m in height. Within the Salicaceae family, seedlings of *Salix atrocinerea* Brot. measure 62 cm in their first year, and those of *Populus tremula* L. 153 cm at two years. Adult individuals of *S. atrocinerea* do not usually exceed 8 m, but the two species of Populus can reach 25 m in height. The seedlings of the Ericaceae family have heights between 61 and 70 cm in their first year of life and between 2.5 and 7 m when they are adults.

Table 2
Average height values of adult plants and seedlings after a disturbance in the early years of native European species. The table indicates the age at which the height of the species is quantified after the disturbance alongside a bibliographic reference. *Data not previously published.

Species	Average adults plants height (m) ***Castroviejo, S. (1986–2012)	Average seedlings or resprouts height after disturbance (cm)	Age	Reference
A. lainzii	3	95	1 year	Cruz et al. unpublished data
A. glutinosa	25	72–108	1 year	(Sopp and Adorján, 1974)
A. unedo	4–7	61	1 year	(Konstantinidis et al., 2006)
B. pendula	30	80	1 year	(Ambroży et al., 2018)
C. sativa	25–30	40.2	2 years	(Marcolin et al., 2020)
		50	18 months	(Catry et al., 2006)
C. siliqua	10	7.5	8 months	(Marques et al., 2001)
C. laurifolius	1–2	20	15 months	(Luis-Calabuig et al., 1996)
		47	46 months	
C. colurna	25	75–87	1 year	(Arslan, 2020)
		430	6 years	(Šeho et al., 2019)
C. multiflorus	1.5	76	1 year	(Reyes and Boedo, 2001)
C. scoparius	1–2	102*	1 year	(Cruz et al., 2020)
		85	1 year	(Hanley, 2009)
C. striatus	3	92*	1 year	(Rivas et al., 2006)
E. australis	2.5	60–70	1 year	(Cruz et al., 2003)
F. excelsior	40	40–50	1 year	(Maltoni et al., 2010)
F. ornus	8–10	93.9	1 year	(Giovannini et al., 1992)
G. scorpius	1.5	58	1 year	(Gazol et al., 2017)
H. lasianthum	1.5–2	15	1 year	(Fernández and Vega, 2014)
O. europaea	8–10	90	18 months	(Catry et al., 2006)
		232		(Negash and Bornman, 2004)
		40	4 years 23 weeks	
P. latifolia	8	97.7	1 year	(Giovannini et al., 1992)
P. brutia	20–35	25	3 years	(Thanos and Doussi, 2000)
P. halepensis	20	15	2 years	(De Las Heras et al., 2002)
P. nigra	20–45	10–40	1 year	(Zlatanov et al., 2010)
P. pinaster	20	7.1	1 year	(Calvo et al., 2013b)
		50.5	5 years	
P. pinea	30	200	2.5 years	(Mutke et al., 2012)
P. radiata	30	42.7	1 year	(Tran et al., 2016)
P. sylvestris	40	143–162	2 years	(Siipilehto, 2006)
P. tremula	10–25	153 ± 41	2 years	(de Chantal and Granström, 2007)
P. tridentatum	1	45	1 year	(Reyes et al., 2009)
Q. ilex	27	91.8	1 year	(Giovannini et al., 1992)
Q. pubescens	25	20	7 months	(Fotelli et al., 2000)
Q. robur	30	85	1 year	(Colin Prentice and Helmisaari, 1991)
S. atrocinerea	8	62*	1 year	(Cruz et al., 2020)
S. junceum	3.5	30–35	5 months	(Roşca et al., 2018)
S. aucuparia	15	55–62	1 year	(Zywiec and Holeksa, 2012)
S. torminalis	25	40	1 year	(Pyttel et al., 2013)
U. europaeus	2.5	75	1 year	(Reyes et al., 2009)
U. minor	2	69	1 year	(Reyes et al., 2009)

***Bibliographic reference.

4. Discussion

Seed viability before germination was very high in all three species; however, *A. dealbata*, which was the species with the highest pregermination viability, also presented greater resistance to fire treatments and maintained its original seed viability practically unaltered with all treatments except the most severe thermal treatments, which caused seed mortality. This behaviour is also shared by other species of the genus Acacia, such as *Acacia longifolia* (Andrews) Willd. and *Acacia mearnsii* De Wild. (Riveiro et al., 2020) and of the Fabaceae family, as occurs in *Paraserianthes lophantha* (Willd.) I.C. Nielsen (García-Duro et al., 2019). The postgermination seed viability of *A. altissima* and *R. pseudoacacia* was reduced with all treatments applied compared to the initial seed viability, following a behaviour parallel to germination, although with slightly higher values. Some fire factors, such as smoke in *A. altissima* or moderate thermal shocks in *R. pseudoacacia*, could have killed pathogens on the seed coat, thus allowing viability after 30 days to barely decrease

in seeds receiving these treatments. Nautiyal et al. (2007) showed that smoke can kill some bacteria harmful to plants, and Kulkarni et al. (2011) indicated that it may also have fungicidal properties.

The germinative behaviours of the seeds of the three studied species are different. In *A. dealbata* and *R. pseudoacacia,* moderate thermal shocks stimulated germination, and severe thermal shocks inhibited germination due to embryo death, as happens in other species of the Fabaceae family, for example, in *Acacia melanoxylon* R.Br. (Arán et al., 2017; Cruz et al., 2017), in *A. longifolia* or in *A. mearsii* (Riveiro et al., 2020). The other treatments left germination at values similar to the value of the control treatment, as Arán et al. (2013) found in *A. melanoxylon* and Kulkarni et al. (2007) in *Acacia hebeclada* DC., *A. mearnsii* and *Acacia robusta* Burch. These species have physical dormancy through the hard coats of their seeds that prevent seed imbibition, and only a small percentage of seeds can germinate without fire (Masaka and Yamada, 2009) or other factors that break the seminal coats (Abdullah et al., 2018; Mirzaei et al., 2013). The expansion and contraction caused by thermal shocks produce cracks in the seminal covers through which water can enter the embryo and, consequently, stimulate germination (Hunt et al., 1999). In this way, it was found that, in some species, thermal shocks not only increase the recruitment of seedlings through the stimulation of germination, but also prevent the seeds from the attacks of microorganisms.

In *A. altissima,* no treatment stimulated germination, and treatments with temperatures above 150 °C nullified the germination of this species. For this reason, *A. altissima* seeds can lose their viability due to denaturation at high temperatures if they are on the surface of the soil (Auld and Denham, 2006; Cheplick and Quinn, 1987) and keep it if buried, even at a depth of a few centimetres (Guthrie et al., 2016; Tozer and Auld, 2006). Smoke and charcoal did not significantly affect the germination of the three IAPs, and ash either reduced or did not modify it. Therefore, *A. dealbata* and *R. pseudoacacia* are fire-dependent species, and *A. altissima* is a fire-sensitive species according to the regeneration model of Reyes and Casal (2008). Of the three species studied, *A. altissima* is the only one that can reduce germination percentage through controlled burns, as moderate thermal shocks greatly reduce germination.

The T_{50} values of *A. dealbata* were between 9 and 13 days, and the values of *A. altissima* were between 8 and 16 days with most treatments tested. Similar germination times were found by Constán (2012) in *A. altissima* seeds from different locations in eastern Spain when subjected to different incubation temperatures; on the other hand, other works on *A. dealbata* found germination times longer than those obtained in this work (Reyes et al., 2015). The average time it takes for half of the total germination to occur in *R. pseudoacacia* was very short. *R. pseudoacacia* obtained T_{50} values between 2 and 4 days with smoke, charcoal and control treatments and 6 days with some heat treatments and Ash3. Masaka and Yamada (2009) studied different heat shocks in soil-buried seeds and control seeds, and Jastrzębowski et al. (2017) studied artificially scarified seeds and obtained very similar germination time values in individuals and populations of *R. pseudoacacia* living in Japan and Poland, respectively. Kheloufi et al. (2018) also found similar mean germination times in *A. dealbata* seeds collected in Algeria with sulphuric acid treatments. Therefore, this trait seems to be quite uniform in seeds from different parts of the world and is not modified by fire. From an ecological point of view, the germination rate of *R. pseudoacacia* is very high, and it germinates slightly faster than the other two IAPs and probably earlier than many native species. Therefore, fire favours the invasibility of *A. dealbata* and *R. pseudoacacia* by stimulating the germination of its seeds. Of the two species, *R. pseudoacacia* also germinates earlier, hence competing better for the establishment of its seedlings as it advances over time. These germinative advantages may explain the large expansion of *R. pseudoacacia* in Europe. Moreover, we found that fire does not favour the germination of *A. altissima*, either by stimulating its germination percentage or shifting it ahead of time. Some heat and ash treatments reduced germination. Consequently, controlled burns could be used to control the germination of *A. altissima*, but it would be necessary to investigate how fire acts on its regrowth.

The requirements for germination and seedling traits are the main components of the regenerative niche and largely determine the success of exotic species in a new environment (McAlpine and Jesson, 2008). Among the native species of Europe living in fire-prone environments, there are examples of species that have very useful regenerative characteristics to compete effectively with the invasive alien plants studied and could be good BSs of IAP. Thus, species of the Fabaceae and Cistaceae families have hard seeds and form seed banks in the soil that persist for many years, and their germination is stimulated by fire. Other species, such as *B. pendula* and *S. atrocinerea*, do not form persistent banks but produce a large number of seeds that can germinate quickly (Cruz et al., 2019; Reyes et al., 1997). There are also species such as *F. excelsior*, *P. latifolia*, *P. brutia*, *P. halepensis*, *P. nigra*, *P. pinaster*, *P. sylvestris*, *Q. pubescens* or *U. glabra* that have very high control germination percentages (above 90%). *P. alba* or *P. tremula* combine the above two features. The germination rate determines who first occupies the space and hoards the resources. Among the selected native species, those that germinated the fastest were *H. lasianthum*, *P. nigra*, *S. atrocinerea* and *U. glabra*. Nevertheless, *A. dealbata*, *A. altissima* and *R. pseudoacacia* also demonstrate very rapid germination.

Light is an environmental factor that influences the emergence, development, establishment and survival of seedlings (Quero et al., 2008; Sack, 2004; Sánchez-Gómez et al., 2008, 2006; Venier et al., 2013). The height reached by seedlings in the early stages of life is another key feature in competing with the seedlings of IAPs and reducing their growth through shading. The three IAPs studied require well-lit areas to live (Aguilera et al., 2015; Kowarik, 1995; Radtke et al., 2013), so shading produced by seedlings of other species will impede their fitness. Rodríguez et al. (2017) noted that the natural shrublands of southwestern Europe, dominated by Fabaceae and Cistaceae shrubs, could be an effective barrier to stem the invasion of *A. dealbata*. However, the pine forests of *P. pinaster*, ecosystems with much greater radiation input, do not impede its advance. Two-year-old seedlings of *A. dealbata* reach between 40 and 70 cm high (Rodríguez et al., 2017), one-year-old seedlings of *R. pseudoacacia* 55 cm (Li et al., 2008) and two-year-old seedlings of *A. altissima* 172 cm (Pan and Bassuk, 1986). In the adult state, *A. dealbata* can reach 25 m (May and Attiwill, 2003), *R. pseudoacacia* reaches 25 m (Zhang et al., 2012) and *A. altissima* grows to over 20 m (Kowarik, 1995). Seedlings of native trees such as *A. glutinosa*, *B. pendula*, *C. colurna, F. ornus*, *O. europaea*, *P. latifolia*, *P. pinea*, *P. sylvestris*, *P. tremula* and *Q. ilex* grew faster than the seedlings of the three IAPs and could overshadow them. In addition, Poorter et al. (2006) found positive relationships between tree height and crown length in mixed forest trees in Bolivia. In the adult state, *A. glutinosa* and *C. colurna* reach 25 m in height, *Q. ilex* 27 m, *B. pendula* and *P. pinea*

30 m, and *P. sylvestris* 40 m. These 6 native tree species could be good competitors of the 3 IAPs in both the seedling and adult phases, but only *C. colurna*, *P. sylvestris* and *Q. ilex* germinate abundantly, with or without stimulant treatment. Among the native shrubs that best compete with the 3 IAPs are *A. lainzii*, *C. multiflorus* and *C. striatus*. Furthermore, these shrubs have hard seeds that form persistent seed banks and have very high germination rates after fire. Owing to this, the three species form very dense and tall stands during the first years after fire (Cruz et al. unpublished data, Reyes and Boedo, 2001; Rivas et al., 2006). Fill et al. (2017) noted that combining management techniques such as the integrated use of fire and active re-seeding of cleared areas with native shrubs would substantially increase the effectiveness of ecosystem restoration.

5. Conclusion

Using the regenerative niche characteristics of native species to control invasive plants through germination rates, plant growth and canopy shading is suggested as a very useful tool. A good combination of shrub and tree species that germinated profusely, grew rapidly after fire and reached great height in adulthood could be the most effective ecological measure to combat the invasion of IAP in newly burned areas. For these reasons, we propose sowing seeds of these BSs in newly burned areas, combining them according to their natural range of geographical distribution and using both shrub and tree species. The shrub species mentioned above compete very well in the early stages after fire and form persistent seed banks from which they generate new plant cohorts in the event of fire. Selected tree species compete well thanks to their adult height. These results open the door to new research addressing field experimentation with barrier species.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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